

INTRODUCTION

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The family Bovidae, which includes Antelopes, Cattle, Duikers, Gazelles, Goats, and Sheep, is the largest family within Artiodactyla and the most diverse family of ungulates, with more than 270 recent species. Their common characteristic is their unbranched, non-deciduous horns. Bovids are primarily Old World in their distribution, although a few species are found in North America. The name antelope is often used to describe many members of this family, but it is not a definable, taxonomically based term.

Shape, size, and color: Bovids encompass an extremely wide size range, from the minuscule Royal Antelope and the Dik-diks, weighing as little as 2 kg and standing 25 to 35 cm at the shoulder, to the Asian Wild Water Buffalo, which weighs as much as 1,200 kg, and the Gaur, which measures up to 220 cm at the shoulder. Body shape varies from relatively small, slender-limbed, and thin-necked species such as the Gazelles to the massive, stocky wild cattle (fig. 1). The forequarters may be larger than the hind, or the reverse, as in smaller species inhabiting dense tropical forests (e.g., Duikers). There is also a great variety in body coloration, although most species are some shade of brown. It can consist of a solid shade, or a patterned pelage. Antelopes that rely on concealment to avoid predators are cryptically colored. The stripes and blotches seen on the hides of Bushbuck, Bongo, and Kudu also function as camouflage by helping to disrupt the animals' outline. Sociable species that live in the open tend to have bold markings or a dark color which, along with conformation, help them to tell their own kind apart from all other species. The sexes may be differently colored, with males usually having the darker pelage (e.g., Sable Antelope). Frequently within species, there are also age-specific colorations.



Figure 1. Variety of size, weight, and body shape in Bovids: (1) Royal Antelope (*Neotragus pygmaeus*); (2) Kirk's Dik-dik (*Madoqua kirkii*); (3) Nubian Ibex (*Capra nubiana*); (4) Sable Antelope (*Hippotragus niger*); (5) Gaur (*Bos gaurus*). Sizes compared to an adult human.

Horns: One of the defining characteristics of the family Bovidae is the presence of unbranched horns (figs. 2 and 3). Horns are present in males of all Bovid species and in females of some genera, usually in large species. Horns in males are always thicker and more complex. The horns are permanently attached to the frontal bones of the skull, and are composed of a bone core covered with a keratin sheath which is never shed, with an air space separating these two layers. Horn size and shape vary greatly, often having a spiral, twisted, or fluted form. This unique horn structure is the only unambiguous morphological feature of Bovids that distinguishes them from other ruminants. *Tetracerus* is unique among wild Bovids in that males regularly bear four horns (two pairs); all other genera, with the exception of some domestic sheep, have only one pair. Horn growth in Bovids continues throughout the animal's life, and horn size and number of rings (not the annulations seen in some species) may be used for age determination (figs. 5 to 7), although size and quality of horns may be altered by several factors, such as food supply. Horns in young animals may seem quite odd compared with the final stage reached in the adult, and can sometimes resemble those of a very different species. Antlers (fig. 4.1), which are characteristic of the family Cervidae (deer), are not true horns: they are made of bone



Figure 2. Variety of horn shapes and sizes in Bovids: (1) Gemsbok (*Oryx gazella*); (2) Addax (*Addax nasomaculatus*); (3) Transcaspiian Urial (*Ovis arkal*); (4) Kirk's Dik-dik (*Madoqua kirkii*); (5) Eastern White-bearded Wildebeest (*Connochaetes albojubatus*); (6) Common Eland (*Taurotragus oryx*); (7) Alpine Ibex (*Capra ibex*); (8) Northern Grant's Gazelle (*Nanger notata*); (9) Mountain Goat (*Oreamnos americanus*); (10) Red Hartbeest (*Alcelaphus caama*); (11) Ellipsen Waterbuck (*Kobus ellipsiprymnus*); (12) Four-horned Antelope (*Tetracerus quadricornis*); (13) Red-flanked Duiker (*Cephalophus rufilatus*); (14) Cape Buffalo (*Syncerus caffer*). Not to the same scale.

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Figure 3. Horns: Horns are composed of a bony core (1) covered with a sheath of keratin (2). They are never branched, although they do vary in shape and size. Neither the sheath nor the core is ever shed, and in many species, the horns never stop growing. Horn cores begin as small bony growths under the skin, over the skull. Found only in Bovids. Photo credits: *Falln-Stock*.



Figure 4. Antlers (1): Consist of bony outgrowths from the skull with no covering of keratin, usually large and branched, growing from an attachment point on the skull called a pedicel. While an antler is growing it is covered with highly vascular skin called velvet; once the antler has achieved its proper size, the velvet is lost and the antler's bone dies. Antlers shed after each mating season. Found only in Cervids. **Pronghorns (2):** They differ from the horns of Bovids in two respects: they are branched, and, while the horns consist of a bony core and keratinous sheath, the sheaths are shed annually, while in Bovids, the sheaths are always permanent. Found only in the Pronghorn antelope. **Ossicones (3):** Giraffes have a pair of short, unbranched, permanent bony processes that are covered with skin and hair, called ossicones. They derive from ossified cartilage, as true horn do, but they remain covered in skin and fur, rather than horn, while antlers are derived from bone tissue. Photo credits: *LaTaxidermia.com* and *Skulls Unlimited*.

without keratin, and are not permanent. Antlers will begin growing in the spring and will continue to grow until mating season, which is when they reach their full size. In late winter, the antlers are shed, and males may be without antlers for a few months until the cycle begins again. Antlers are branched and are only found on males (and female Caribou). Horns in the family Antilocapridae, with only a single extant species, the Pronghorn, are different from either true horns or antlers (fig. 4.2), but have characteristics of both: they are made of keratin growing on a bony core, like true horns, but they are shed annually; in addition, the horn sheath is branched in male Pronghorns, while true horns are always unbranched. Giraffes (family Giraffidae) have a pair of short, unbranched, permanent bony processes that are covered with skin and hair, called ossicones (fig. 4.3); they differ from horns in Bovids in that they do not project from the frontal bones, but lie over the sutures between the frontal and parietal bones. Rhinoceros horns differ from true horns because these horns have no core or sheath; they are made up of a multitude of epidermal cells and bundles of dermal papillae, extensions of the dermis, forming horny fibers similar to thick hair. A single horn is situated over the nasal bones;



Figure 5. Horn growth in male Black-faced Impala (*Aepyceros petersi*): Age can be estimated by rings on horns. Note that horns of young animals may seem quite odd compared with the final stage reached in the adult, and can sometimes resemble those of a very different species.

and in species that have two horns, the second horn lies over the frontal bones. Other ungulates may have tusks, which are elongated, continuously growing front teeth, that may protrude well beyond the mouth; they are most commonly canines, as with warthogs and pigs.

Hooves (fig. 8): Keratinous hooves sheathe the terminal bone of each toe. Hooves are modified toenails, and are composed of two structures: the unguis and the subunguis, which connect the unguis to the pad of the digit. Unlike claws and nails, hooves are the principal point of contact between the legs and the ground; as a result, ungulates are said to have unguligrade limbs. The tough unguis encircles the tip of the digit as a cylinder, enclosing the subunguis within it. Since the unguis is harder than the subunguis, it does not wear down as quickly, resulting in a firm leading edge to the hoof. Bovids walk on their hooves and have paraxonic feet, in which two well-developed digits, the third and fourth digits, bear the weight of the body. The second and fifth digits are either absent or, more often, small, forming the so-called lateral hooves, or dewclaws. The third and fourth metapodials, the only ones completely present, are fused into a single functional unit sometimes referred to as the cannon bone. Bovids walk primarily in diagonal couplets. They also trot, and larger forms can canter.

Skeletal System (figs. 9 and 10): The premaxillae exist as separate elements and often suture with nasals as well as with the maxillae. The orbits are fully ringed with bone, which generally is tubular. A single lacrimal canal is usually present in the orbits of the skull. There is no sagittal crest in the skull. Horns emerge above and behind the orbits, on the frontal bones. The interfrontal suture is obvious. An interparietal bone is present. The upper incisors are absent and the upper canines are either reduced or absent. Instead of upper incisors, Bovids have an area of tough, thickened tissue known as the dental pad, which provides a surface for gripping plant materials. The lower incisors project forward and are joined by modified canines that emulate the incisors. These modified incisors are followed by a long toothless gap known as a diastema. Bovids have a generalized dental formula of $I\ 0/3, C\ 0/1, P\ 3/3, M\ 3/3 \times 2 = 32$. Age of Bovids may be determined by examination of the teeth. There are 7 cervical, 13 thoracic, 6 to 7 lumbar, 4 to 5 sacral, and 16 to 20 caudal vertebrae. Clavicles are absent. The scapulae are long, oblong in shape, with prominent cartilaginous dorsal margins. The ulna is fused with the radius and the fibula with the tibia. The navicular is fused to the cuboid in the tarsus. Metapodials III and IV are fused along the midline, and II and V are rudimentary. Phalanges III and IV are shortened. The phalanges are enclosed in hooves; in the case of the rudimentary phalanges of II and V, the distal ones are encased in small hooves.

Feeding and Digestive System: Most Bovids are herbivorous, except Duikers, which may be

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Figure 6. Horn growth in male European Mouflon (*Ovis aries musimon*): Age can be estimated by rings on horns (but not the annulations seen in some species). Growth is slow in winter. Size increases up to 8 years. It must be noted that techniques that rely solely on horn size for estimation of age may be unreliable.



Figure 7. Horn growth in Blue Wildebeest (*Connochaetes taurinus*): Age can be estimated by horn shape and length, as there are no rings. Horns are present in both sexes, although those in females are thinner.



Figure 8. Hooves in Even-toed Ungulates (Artiodactyla): Weight is borne by the III and IV toes (paraxonic limb structure): (1) Family Giraffidae (*Giraffa camelopardalis*) without dewclaws; (2) Family Camelidae (*Camelus dromedarius*) with toenails instead of hooves; (3) Family Bovidae (*Syncerus caffer*); (4) Family Suidae (*Sus scrofa*) with four toes, although they walk only on the middle two digits; (5) Family Hippopotamidae (*Hippopotamus amphibius*) with pads instead of hooves and four toes, all of them used in walking. **Hooves in Odd-toed Ungulates (Perissodactyla):** Weight is mostly or entirely borne by the III toe, featuring an odd number of toes on the rear feet: (6) Family Rhinocerotidae (*Ceratotherium simum*) with three foot pads with nails; (7) Family Equidae (*Equus ferus*). Not to the same scale.

omnivorous. Bovids obtain their food by browsing or grazing, subsisting on plant material. Plants such as grasses and forbs are brought into the mouth by the lips and tongue, where they are severed by the lower incisors pressing against the hard cartilaginous pad of the upper palate, followed by a quick upward jerk of the head. Tougher plants such as shoots of shrubs are severed by the premolars and molars. Depending on diet, the incisors can be wide (spatulate) and relatively uniform in size, as in grazers, or narrower and often of various sizes, as in browsers. Ruminants' digestive system is characterized by functional and anatomical adaptations that allow them to unlock otherwise unavailable food energy in fibrous plant material, mainly in cellulose. This property gives them an advantage over non-ruminants. An important characteristic of ruminants' digestive system is the occurrence of microbial fermentation prior to gastric and intestinal digestion activity. Their unique digestive system integrates a large microbial population with the animal's own system in a symbiotic relationship. The microbial fermentation occurs mainly in the rumen, the first chamber of the four-compartment stomach, which consists also of the reticulum and omasum (act as filters), and the abomasum (the true enzymatic stomach).

Scent glands: Dense cluster of cells, generally flask shaped, derived from hair follicles. Their chemically complex secretions convey information about the individual's identity, sex, age, and social and reproductive status. The most common and important scent glands are the hoof or interdigital glands and the preorbital glands. The secretions of the hoof glands, exuding from the cleft between the hooves, leave a scent trace that helps antelopes follow one another. Preorbital glands are employed mainly for marking objects. Female Bovidae have either one or two pairs of functional mammae.

Sexual dimorphism: Most Bovids are sexually dimorphic. Adult males and females of a species

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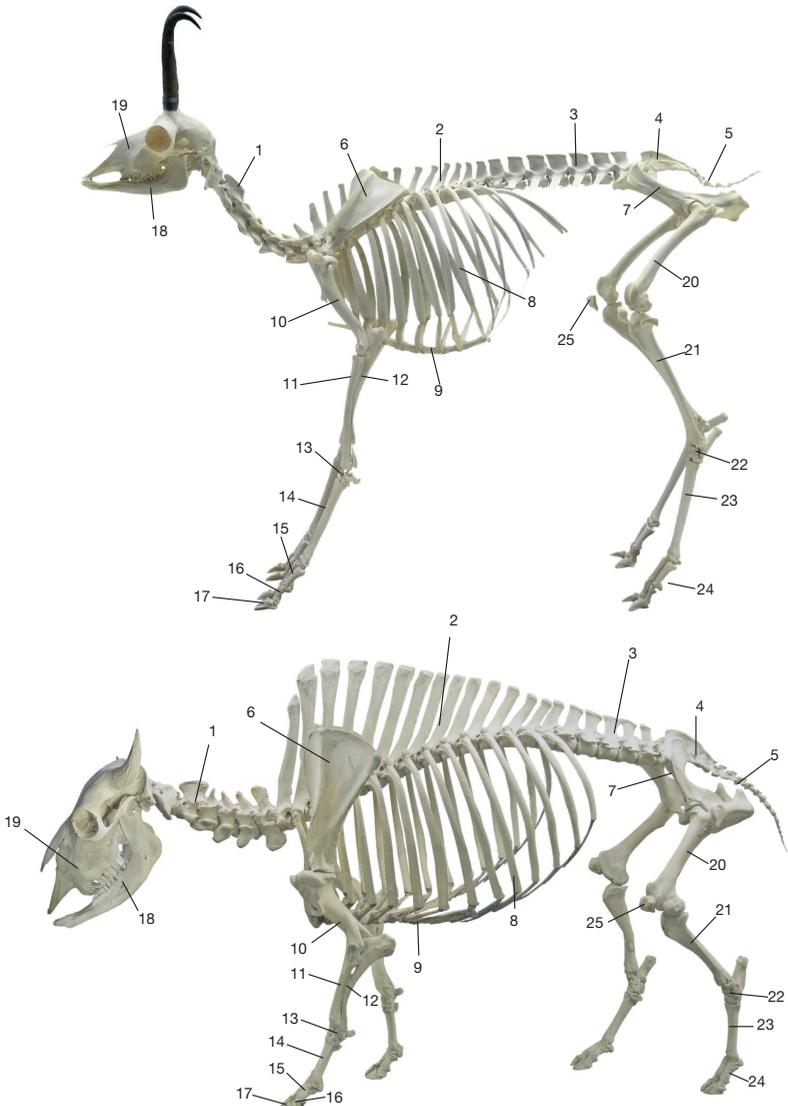


Figure 9. The skeleton of an Alpine Chamois (*Rupicapra rupicapra*) and an American Bison (*Bos bison*): (1) Cervical vertebrae; (2) dorsal vertebrae; (3) lumbar vertebrae; (4) sacrum; (5) coccygeal (caudal) vertebrae; (6) scapula; (7) ilium; (8) ribs; (9) sternum; (10) humerus; (11) radius; (12) ulna; (13) carpus; (14) metacarpus; (15) proximal phalanx; (16) middle phalanx; (17) distal phalanx; (18) mandible; (19) maxilla; (20) femur; (21) tibia; (22) tarsus; (23) metatarsus; (24) phalanges; (25) patella. Not to scale. Photo credits: Smithsonian.

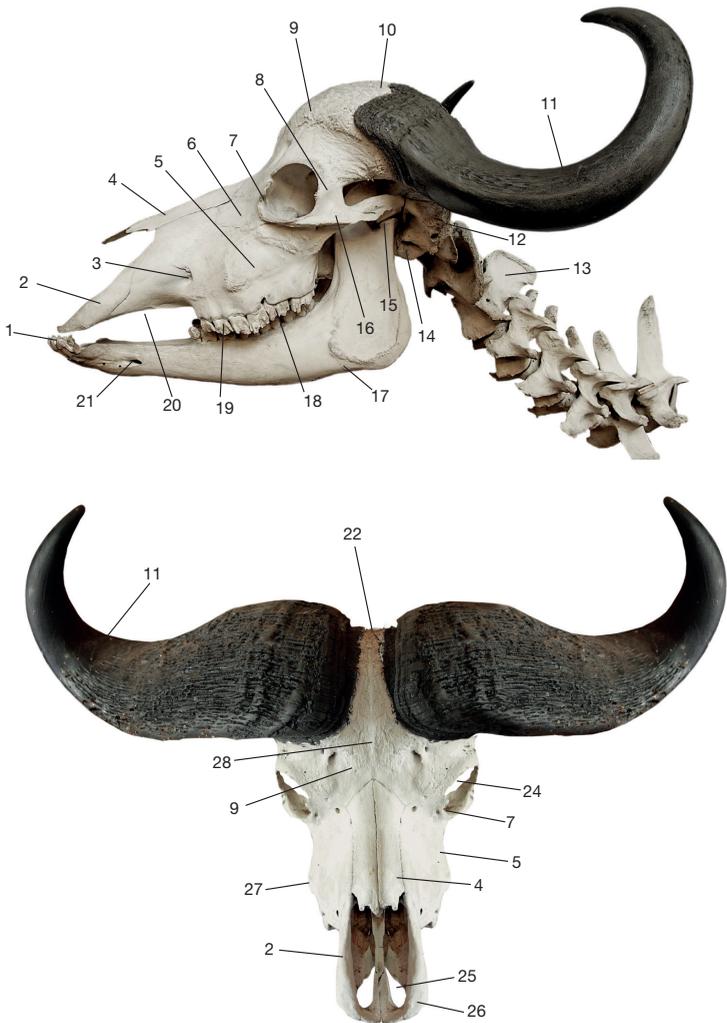


Figure 10. The skull of a Cape Buffalo (*Syncerus caffer*): (1) Lower incisors; (2) incisive bone (premaxilla); (3) infraorbital foramen; (4) nasal bone; (5) maxilla; (6) lacrimal bone; (7) fossa for lacrimal sac; (8) postorbital bar; (9) frontal bone; (10) cornual process; (11) horn; (12) occipital bone and condyle; (13) cervical vertebrae; (14) tympanic bulla; (15) condylar process of mandible; (16) zygomatic bone; (17) mandible; (18) molars; (19) premolars; (20) diastema; (21) mental foramen; (22) intercornual protuberance; (23) supraorbital foramen; (24) orbit; (25) palatine fissure; (26) body of incisive bone; (27) facial tuber; (28) sagittal crest. Photo credits: *Jebulon*, Muséum National d'Histoire Naturelle (Paris), *Boleslaw Kubica*.

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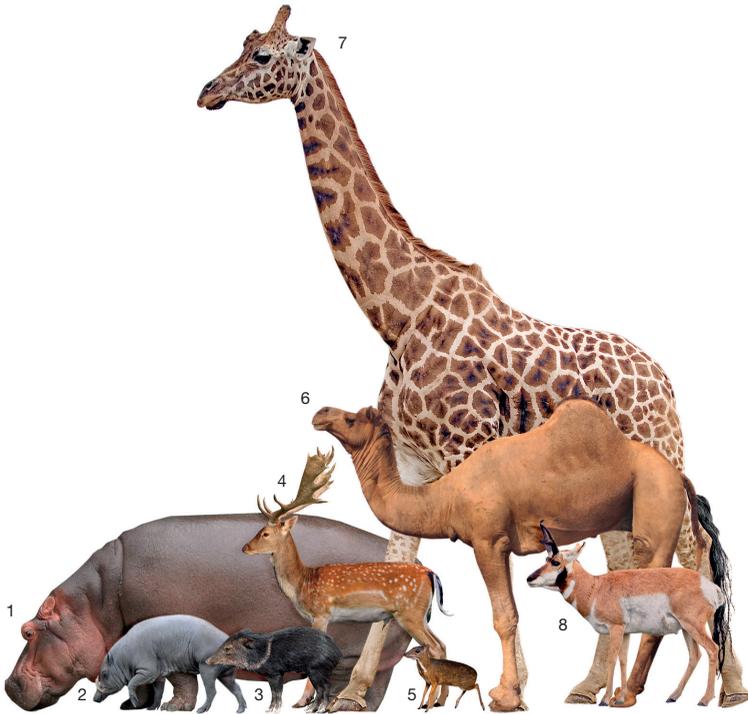


Figure 11. Non-bovid Artiodactyls (from left to right): (1) Hippopotamidae (*Hippopotamus amphibius*), (2) Suidae (*Babyrousa celebensis*), (3) Tayassuidae (*Pecari tajacu*), (4) Cervidae (*Dama dama*), (5) Tragulidae (*Tragulus kanchil*), (6) Camelidae (*Camelus dromedarius*), (7) Giraffidae (*Giraffa camelopardalis*), and (8) Antilocapridae (*Antilocapra americana*). To the same scale. Photo credits: *Kol Tregaskes* (London Zoo), *Jeff Whitlock* (San Antonio Zoo), *Ken Trease, Samson, Dibrova*.

may differ in size, color, shape, or development of horns or scent glands. This is the result of male reproductive competition, which causes males to acquire physical and behavioral traits that enhance their ability to compete successfully with other males. The most striking sexually dimorphic characters in Bovids are size and development of horns. Bovids with polygynous reproductive systems, those that are diurnal, and open-habitat dwellers tend to present a greater sexual dimorphism. In monogamous systems, male sexual competition is minimal and consequently there is little dimorphism, and females may be slightly larger than males, as in Duikers and dwarf antelopes. Size dimorphism is much greater in Bovids of medium and large size, where males mature much later than females. Dimorphism is particularly well developed in Reduncini (Kob, Lechwe), Tragelaphini (Kudu, Eland), and Caprini (Ibexes and Goats). On the contrary, Alcelaphini (Hartebeest, Wildebeest) and Hippotragini (Oryxes, Roan Antelope) have little dimorphism. These species, though polygynous, share the tendency to form mixed herds containing adults of both sexes, and are usually under ecological pressure to integrate. Color dimorphism is less common than size or horn dimorphism, and in some Bovids adult males become much darker than adult females. Males also have better-developed scent glands than females.

TAXONOMY

The definition of a species and subspecies is subject to constant debate and revision by biologists, resulting in changes in the official lists of Bovid species. The taxonomy of the Bovidae stabilized after Ellerman in 1953, with little change by Ansell in 1972, and was based on the Morphological Species Concept, in which organisms are classified in the same species if they appear identical by

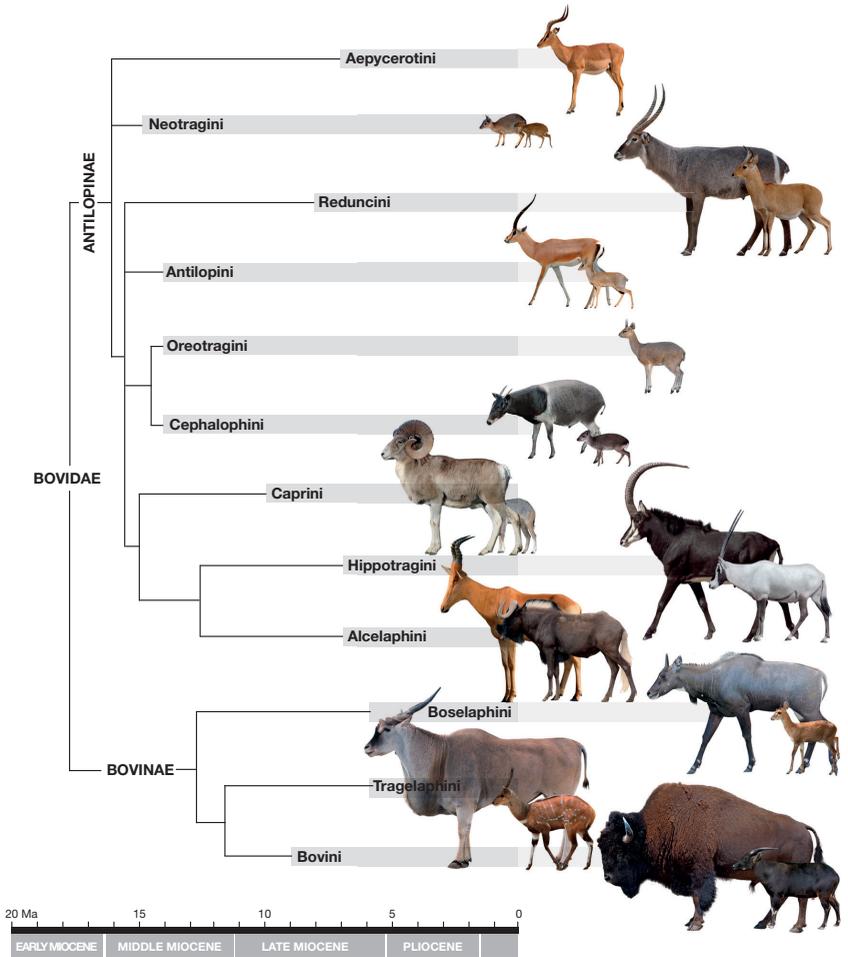


Figure 12. Systematic classification of the family Bovidae: Phylogenetic diagram charting the evolution of the major Bovid clades: the subfamily Antilopinae is very diverse, and its tribes are very distinct from one another, ranging from the smallest to medium and large-sized forms, usually smaller and more lightly built than many of the Bovinae; its horns are transversely ringed, and there are almost always prominent glands in front of the eye and in the forehead. Most of them, except Cephalophini and Neotragini, live in open country or light cover. The subfamily Bovinae includes three well-distinguished tribes, with medium to very large species, usually heavily built and thick legged, with horns lightly or strongly spiraled, not ringed as in Antilopinae, and pelage with less contrast in color. They are usually adapted to heavy cover or deep forest. To the same scale. Modified from *Bibi, Bukhsianidze, Gentry, Geraads, Kostopoulos, and Vrba, 2009*.

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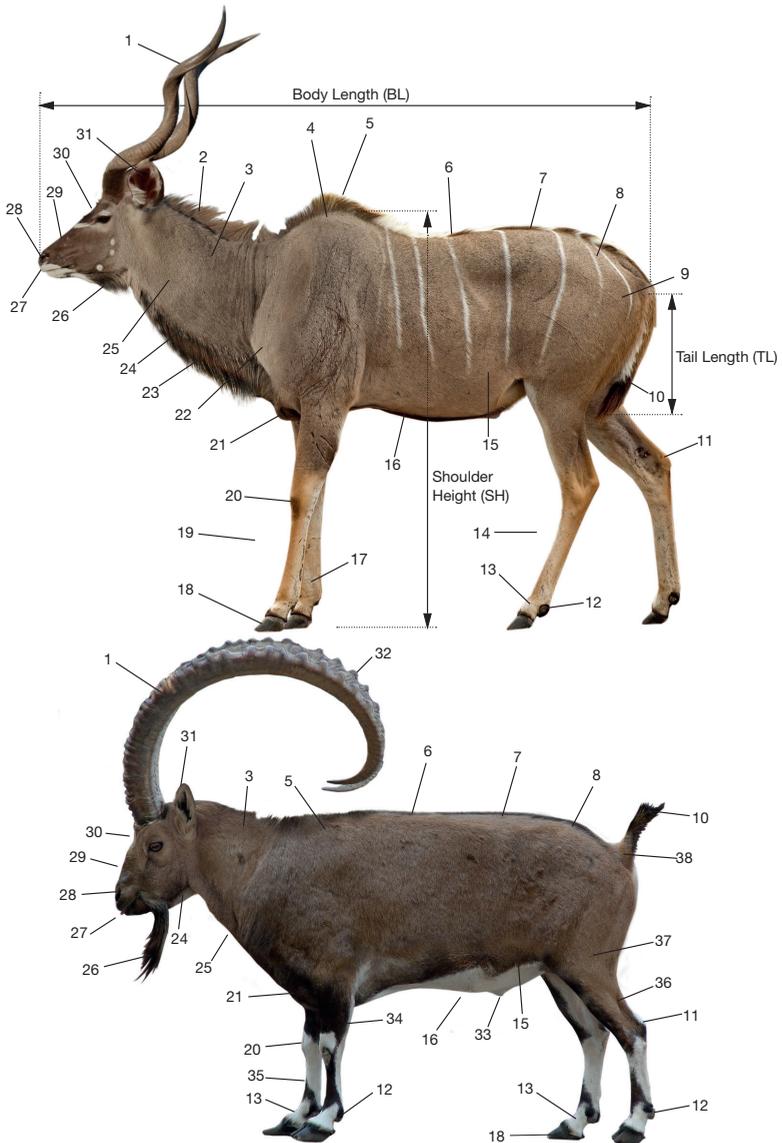


Figure 13. Topography of Zambezi Greater Kudu (*Tragelaphus strepsiceros*) and Sinai Ibx (*Capra nubiana*): (1) Horns; (2) nape mane; (3) neck; (4) top of shoulders; (5) withers; (6) chine; (7) loin; (8) rump; (9) buttock; (10) tail; (11) hock; (12) dewclaw; (13) pastern; (14) hind leg; (15) flank; (16) belly; (17) fetlock; (18) hoof; (19) foreleg; (20) knee; (21) brisket; (22) chest; (23) throat mane; (24) dewlap; (25) throat; (26) beard; (27) muzzle; (28) nostril; (29) bridge of the nose; (30) forehead; (31) ear; (32) horn rings; (33) sheath; (34) forearm; (35) cannon; (36) shank; (37) thigh; (38) tail head. Photo credit: Gerrit De Vries and Sergey Chichagov.

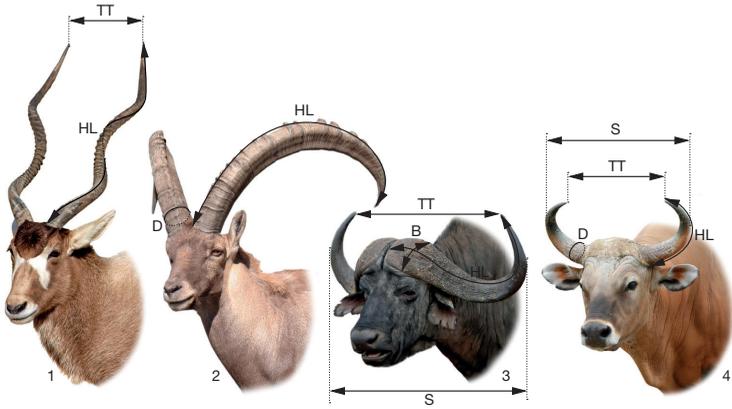


Figure 14. Horn measurements: HL: horn length, TT: tip to tip distance, D: horn diameter, S: horn spread, B: boss. For spiral horns (1), horn length (HL) is measured around the spiral, keeping the tape on top of the spiral ridge, starting at the lowest point at the front of the base and proceeding to the tip. For Ibexes (2), HL is measured from the lowest point in front of the tip. For Cape Buffalo (3), Wildebeest, and Muskox, HL is measured from the center of the boss to the tip following along the center of the horn surface. For European and Asian Wild Cattle (4), HL is measured from the lowest point on the underside along the outside curve to the tip. Horn diameter (D) is measured at right angles to the axis of the horn, usually at the base. Horn spread (S) is measured at the greatest distance between horns. Boss (B) is measured at the greatest width. Photo credits (1) *Alex Meyer*, San Antonio Zoo (USA), (2) *Alex Meyer*, Munich Zoo (Germany), (3) *Duncan Noakes*, (4) *Pierre de Chabannes*, Khao Kheow Open Zoo (Thailand). Not to the same scale.

morphological criteria, and on the Biological Species Concept, which defines a species as members of populations that interbreed in nature, but not necessarily according to similarity of appearance. However, new evidence and shifting opinions have led to changes in this traditional classification. Groves and Grubb, applying the Phylogenetic Species Concept, in which a species is defined as the smallest population or group of populations displaying diagnostic, genetically based differences compared to other populations, revised the entire scope of hoofed mammals in 2011, and reclassified many subspecies of Bovids as full species. We have followed this approach in this book.

The application of the Phylogenetic Species Concept has increased the number of Bovid species so significantly that they may be perceived by some readers as surprising. This approach has brought to light a number of overlooked taxa, which may inadvertently have escaped deserving attention from scientists for decades through the 20th century, and which may face extinction in a matter of several years (e.g., *Hippotragus variani*, *Alcelaphus tora*, *Oreotragus porteousi*, *Ovis nigrimontana*). In addition, this approach emphasizes the conservation significance of ecosystems (e.g., Serengeti-Mara, Cape Region, Sudan Grasslands, Bangweulu-Upemba wetland complex).

Readers are encouraged to remain open to new findings and to be aware of the fact that taxonomy does not and probably for some time will not give definite answers with respect to Bovids. Even if some of our readers refuse the elevation of some subspecies into species, they are given the chance to see that the taxa actually represent different animals which should definitely not be forgotten.

CLASSIFICATION

Bovids belong to the taxonomic order Artiodactyla (fig. 11), also known as even-toed ungulates. This order includes nine families: Suidae (pigs), Tayassuidae (peccaries), Hippopotamidae (hippos), Camelidae (camels and llamas), Tragulidae (mouse deer), Giraffidae (giraffe and okapi), Antilocapridae (pronghorn), Cervidae (deer), and Bovidae. Close to 65% of the extant species of Artiodactyls are in the Bovidae. Suidae and Tayassuidae are distinguished from Bovidae by the absence of horns, the presence of four toes on each foot (although they walk only on the middle two digits), a simple stomach, and a compact body with an elongated head ending with a naked nasal disc. Hippopotamidae are stout, naked-skinned, amphibious Artiodactyls, possessing three-chambered

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stomachs (pseudoruminants) and walking on four toes on each foot. Camelidae may be distinguished from Bovidae by the absence of horns and hooves (they have two-toed feet with toenails and soft foot pads), a different dentition (presence of upper incisors and upper canines), a three-chambered stomach, and a different musculature of the hind limbs. Tragulidae are small ungulates with no horns or antlers, four complete digits in all limbs, a three-chambered stomach, and tusk-like upper canines. Cervidae are recognized by the antlers, usually complexly branched, in males of most species. Female Cervids may be distinguished from Bovids by a combination of characters in the lacrimal bone; otherwise, they may look similar. Antilocapridae contains only one living species, the Pronghorn (*Antilocapra americana*); as in Bovidae, they have a four-chambered stomach, cloven hooves, a similar body shape to antelopes, a similar dental formula, and their horns resemble those of the Bovids, although they are branched and shed outside of the breeding season, and subsequently regrown. Giraffidae, which is composed of two genera: *Giraffa* (giraffes) and *Okapia* (okapi), may be recognized by the presence of ossicones instead of horns, the long limbs and neck, and a sloping body profile.

Systematic work on Bovids has been difficult, as it is one of the most troublesome groups of mammals to classify. Molecular studies have concluded the existence of a major division within the family Bovidae, with two main subfamilies: Antilopinae and Bovinae (fig. 12):

SUBFAMILY ANTILOPINAE: Includes nine tribes, which are very distinct from one another: Hippotragini, Alcelaphini, Reduncini, Cephalophini, Neotragini, Oreotragini, Aepycerotini, Antilopini, and Caprini. Horns in this subfamily are transversely ringed, and there are almost always prominent glands in front of the eye and in the forefeet.

Tribe Aepycerotinae: Consists of a single genus, the Impalas. Aepycerotinae is endemic to Africa. Impalas are sexually dimorphic, as only males possess horns.

Tribe Neotragini: Often referred to as dwarf antelopes, which are among the smallest ungulates, and includes only one genus: *Neotragus*. They are primarily forest-dwelling species, with a hare-like build, with long and slender legs, large eyes, and small muzzles. They have short, vertical, spike-like horns, found only in males, never in females. They have facial and inguinal glands; preorbital glands lack a surface fold of skin.

Tribe Reduncini: Includes Reedbucks, Lechwes, Kobs, Waterbucks, Rheboks, and relatives, primarily distributed throughout parts of Africa. Species in Reduncini are medium to large-sized grazers that often have strong ties to water. They also have long hair, and all species exhibit sexual dimorphism, as horns are only present in males.

Tribe Antilopini: Often referred to as true antelopes, includes small to medium-sized species, in native to open, arid environments in Africa and Eurasia, but occur in particularly high densities in East Africa. This tribe includes true Gazelles (genera *Eudorcas*, *Gazella*, and *Nanger*), *Procapra* (which appear to be as different from the Gazelles as they are from the dwarf antelopes), Saiga, and dwarf antelopes (*Dorcatragus*, *Madoqua*, *Ourebia*, and *Raphicerus*). There is little sexual dimorphism, and horns are generally present in both sexes. There are often striking markings on the face, flanks, and/or rump. Preorbital glands are well developed in most species.

Tribe Oreotragini: Represented by one living genus, the Klipspringers. They are small, stocky antelope, with females weighing more than and being slightly longer than males. Their hoof structure is unique because the last joints of the digits are rotated so they can walk on the tips of their hooves. Only the males have horns, except for one species.

Tribe Cephalophini: Consists of several species of Duiker. Duikers are highly specialized and are resident in the tropical forests of Africa. They are easily recognizable as they have the same basic body plan but differ significantly in size. Unlike in most Bovids, females are slightly larger than males. Also unlike most other Bovids, Duikers are primarily frugivorous.

Tribe Caprini: Consists of Goats, Sheep, Muskox, and relatives. Taxonomy of this tribe is complex and several classifications have been suggested. Most authors recognize four distinct groups: Sheep and Goats; Muskox and Takin; Serows, Gorals, and Chamois; and Tibetan Antelope. Caprini are especially adapted to montane and alpine environments, which explains why this is the only tribe that is more diverse in Eurasia than in Africa. In general, both genders have horns; however, horn morphology in many species is sexually dimorphic.

Tribe Hippotragini: This tribe consists primarily of large grazing antelopes with large horns: Oryxes, Addax, Sable, and Roan Antelopes. Hippotragini species are restricted to Africa and east-central Asia

and are primarily grazers. Most species live in arid habitats and have an erect mane along the nape of the neck.

Tribe Alcelaphini: Includes Wildebeests, Hartebeests, Topis, Tsessebes, Blesbok, and relatives. All of the species in this tribe are nomadic grazers that are native to Africa. Most species are size-dimorphic, with males being larger than females, and both bearing double-curved (lyrate) horns.

SUBFAMILY BOVINAE: Includes three tribes: Bovini (cattle and Buffalo), Tragelaphini (spiral-horned antelopes), and Boselaphini (Nilgai, Four-horned Antelope). Sexual dimorphism is highly prevalent in this subfamily, with the males of some species weighing nearly twice as much as their female counterparts. Bovines have played an important role in the cultural evolution of humans, as numerous species within this subfamily have been domesticated for subsistence purposes.

Tribe Boselaphini: Includes only two species, both from India: Nilgai and Four-horned Antelope, which do not appear to be closely related. They are sexually dimorphic, and only males have short, smooth, conical horns. This tribe and the Saola are the only Bovinae that have facial glands.

Tribe Tragelaphini: A group of medium-sized to large antelopes, with spiral or twisted horns, white vertical stripes, and significant sexual dimorphism. Horns are found in the males of all species, while most females are hornless, except in the larger forms: Elands and Bongo.

Tribe Bovini: Includes three subtribes: Bovina (cattle and Bison), Bubalina (Buffalo), and Pseudoryina (only represented by the recently discovered Saola). They are usually large, massive, heavy-bodied animals, with short, thick legs, and smooth rather than annulated horns. There is significant sexual dimorphism, with males usually bigger than females. Horns are present in both sexes.

EVOLUTION AND FOSSIL RECORD (fig. 12)

Bovids are the most diverse ungulates, and their evolutionary history is similarly diverse. Evolution within this family is characterized by adaptive radiations, global migrations and mass extinctions, and today there are about 270 extant species of Bovids recognized. Until now, the impressive fossil record has revealed more than 300 extinct species or ancestors of modern species. However, the current knowledge on earliest Bovids is quite limited. Bovids diverged from Cervids and Giraffids in Eurasia, near the Oligocene/Miocene boundary approximately 23 Ma, due to the evolution of a more advanced ruminating digestive system, which allowed these species to exploit a different vegetation base. Cervids evolved in Eurasia from the early Miocene onward, taking to the cooler regions at higher latitudes, while Bovids, firmly established there by the middle Miocene, and were better adapted to warmer temperatures, facilitating their later migration into the African continent as the global climate warmed. *Eotragus*, a small gazelle-like animal with simple, straight horn cores, is considered the first true Bovid, and appeared more or less simultaneously in Europe and Asia at about 18 Ma. Living in woodland savannas, these early Bovids were moderately diverse, with only a few genera.

During the early Miocene, Bovids differentiated into two main lineages: Antilopinae and Bovinae. This divergence was related to a long period of continental separation, in which the Antilopinae would have evolved from Asian stock that migrated into Africa, where they initially specialized in drier habitats and were of a smaller size. Once in Africa they differentiated into tropical and arid types, some of which later returned to Asia and gave rise to the Caprini and to other specialized species. The Bovinae fossil record suggests a South Asian origin, from where they further radiated into Boselaphini, Bovini, and Tragelaphini. Tragelaphines migrated into Africa where they have been distinct for at least 15 million years. This explosive tribal radiation during the Middle Miocene, gave rise to the majority of extant Antilopinae and Bovinae tribes.

By the late Miocene, around 10 Ma, Bovids rapidly diversified, partly because many species became adapted to more open, grassland habitat, being able to move rapidly over the open plains, and having high-crowned teeth in order to cope with tough grasses. When the ice sheets advanced during the Plio-Pleistocene a number of Bovids became adapted for cold climates as well. Increased tolerance of cold climate also allowed a few Bovids to cross the Bering land bridge and invade the New World in the Pleistocene (e.g., Muskox, Bighorn Sheep, Mountain Goat). Bovids never reached South America until Europeans introduced domestic cattle and sheep, but Bison did reach as far south as El Salvador.

Aepycerotini first appeared in the late Miocene, and no significant difference between primitive and modern Impalas has been noted. Neotragines also retain many primitive features compared with other members of the Antilopinae, and they seem to have been one of the earliest branches to separate, more than 15 Ma. Reduncini probably diverged from Antilopini in the mid-Miocene, or both diverged

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from undifferentiated early Antilopinae, and they first appeared in the fossil record 7 Ma in Eurasia. Antilopini either originated 17 Ma in Africa, or still-unknown Eurasian ancestors migrated there at an early date; existing Asian and African lineages are distinctly different. Oreotragini are not related to other dwarf antelopes, but are distantly related to Duikers, from which they separated about 13 Ma. The Cephalophini fossil record is scarce, beginning approximately 6 Ma, although some records indicate that this tribe may have been present 12 Ma. Divergence times of most Duikers date to the Pleistocene, when the colder, drier temperatures during glacial maxima might have led to the isolation and subsequent diversification of tropical, forest-associated taxa. Caprini and their relatives Hippotragini and Alcelaphini are an extremely diversified group including several Bovid branches of probably different origin, which makes their supra-generic classification quite delicate. The origin of the tribe is dated back to the early-middle Miocene. Hippotragini, presently restricted to Africa, first appeared in the fossil record 6.5 Ma; they may have originated in Eurasia and then colonized Africa by crossing the Sahara Desert. Alcelaphini are a relatively recent evolutionary development, and the first fossils appear 5 Ma in Africa.

Boselaphini were a successful Eurasian group that appeared during the late Middle Miocene and strongly radiated and expanded during the Late Miocene from China to Europe and Africa; extant Nilgai and Four-horned Antelope are Miocene relicts and are most related to early Bovids. Bovini split off from a Boselaphine ancestral stock on the Indian subcontinent and then they expanded to Africa and Eurasia, invading North America too. Within this tribe, three divergent lineages have been identified: Bovina, Bubalina, and Pseudorygina, which may have diversified during the late Middle Miocene, approximately 13 Ma. Tragelaphini first appeared in the fossil record 6 Ma during the late Miocene.

Research is thus far showing Bovidae to be the most vastly diversified group of hoofed mammals as well as one of the most vastly diversified groups of herbivorous mammals to have inhabited the planet. Bovid fossils are of great use in the study of evolutionary biology and offer clues to patterns of adaptation and evolution.

HOW TO USE THIS BOOK (fig. 15)

The main purpose of this guide is to enable the observer to accurately identify all known species and subspecies of wild and feral Bovids from all over the world. Information is presented in the same format throughout, with maps showing geographic ranges, and photographs highlighting the specific identification criteria in each case. We have packed as much detail into this volume as possible, but also worked hard to keep it concise and efficient, so that it is not unwieldy in the field. All the information for a given species is displayed on two facing pages.

The overall structure of this guide is based on the taxonomic classification of the family Bovidae into tribes, and is organized to provide the maximum ease of use for its readers. To help the reader grasp the scientific arrangement, the pages for each tribe have a distinctive color on their top margin.

With very few exceptions, all the Bovids can be identified from field sightings by using the photographs and descriptions in this guide. Look through the color plates and determine what type of animal you saw. Turn to the text page for the species that most resembles your sighting and look at the distribution map. If the map is not shaded for your area, then return to the color plates and try another similar species or subspecies. Keep in mind that many species may vary slightly in color from one region to another and that not all color morphs can be illustrated in a guide. When you find a species that resembles your sighting and occurs in the correct geographic area, read the text to see if the description fits the habitat that you are in and any behavior you may have observed. Also check the Similar Species section for other possibilities.

Care should be taken when identifying juvenile animals or females as they may differ considerably from the adult males. Shape and development of horns can be especially misleading in the case of Bovids; the horns of young animals may seem quite odd compared with the final stage reached in the adult, and can sometimes resemble those of a very different species.

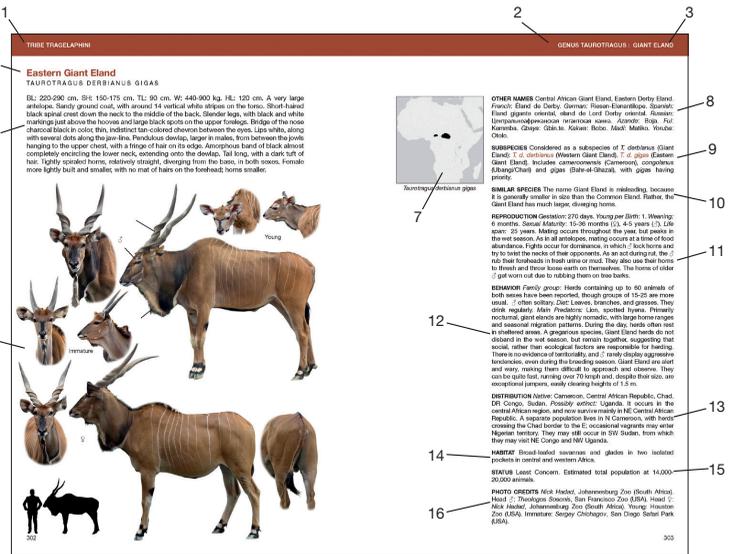


Figure 15. Understanding a page layout: (1) tribe; (2) genus; (3) common name; (4) common and scientific names; (5) measurements and description; (6) color plates and silhouette comparing size with a human figure; photographs of both sexes, young forms, and coat variations are usually included; features that are most important for identification are indicated by bars; (7) distribution map; (8) other names, including foreign and local names; (9) subspecies and taxonomy; (10) similar species or subspecies; (11) reproduction biology; (12) behavior; (13) distribution; (14) habitat; (15) conservation status, based on the IUCN Red List of Threatened Species, and estimated population; (16) photo credits.

ABBREVIATIONS

The following abbreviations, contractions, and symbols have been used in the book to make it simpler for the reader to access the information.

- cm: centimeters
- g: grams
- kg: kilograms
- m: meters
- km: kilometers
- km²: square kilometers
- ha: hectares
- kmph: kilometers per hour
- NP: National Park
- BL: body length
- TL: tail length
- HL: horn length
- Ma: millions years ago
- W: weight, west, western
- N: north, northern
- NE: northeast, northeastern
- NW: northwest, northwestern
- S: south, southern
- SE: southeast, southwestern
- SW: southwest, southwestern
- E: east, eastern
- ♂: male, males
- ♀: female, females
- DR Congo: Democratic Republic of Congo
- Congo: Republic of Congo